

University of Groningen

Foraging in a spatially patterned world

Klaassen, Raymond Hendrikus Gerardus

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2006

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Klaassen, R. H. G. (2006). *Foraging in a spatially patterned world: Migratory swans (Cygnus columbianus) seeking buried pondweed (Potamogeton pectinatus) tubers.* s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Prior knowledge about spatial pattern affects patch assessment rather than movement between patches in tactile-feeding Mallard

Raymond H.G. Klaassen, Bart A. Nolet & Casper H.A. van Leeuwen
submitted



Casper van Leeuwen monitoring the inter-patch movements of a Mallard that is feeding in the adjacent room.

Summary

1. Heterogeneity in food abundance allows a forager to concentrate foraging effort in patches that are rich in food. This might be problematic when food is cryptic, as the content of patches is unknown prior to foraging. In such case knowledge about the spatial pattern in the distribution of food might be beneficial since this enables a forager to estimate the content of surrounding patches. A forager can benefit from this pre-harvest information about the food distribution by regulating time in patches and/or movement between patches.
2. We conducted an experiment with Mallard *Anas platyrhynchos* foraging in environments with random, regular, and clumped configurations of full and empty patches. An assessment model was used to predict the time in patches for different spatial distributions, in which a Mallard is predicted to remain in a patch until its potential intake rate drops to the average intake rate that can be achieved in the environment. A movement model was used to predict lengths of inter-patch movements for different spatial distributions, in which a Mallard is predicted to travel to the patch where it expects the highest intake rate.
3. Consistent with predictions, in the clumped distribution Mallard spent less time in an empty patch when the previously visited neighbouring patch had been empty than when it had been full. This effect was not observed for the random distribution. This shows that Mallard use pre-harvest information on spatial pattern to improve patch assessment. Patch assessment could not be evaluated for the regular distribution.
4. Movements that started in an empty patch were longer than movements that started in a full patch. Contrary to model predictions this effect was observed for all distributions, rather than for the clumped distribution only. In this experiment Mallard did not regulate their movements in relation to pattern.
5. An explanation for the result that pre-harvest information on spatial pattern affected patch assessment rather than movement is that Mallard move to the nearest patch where the expected intake rate is higher than the critical value, rather than to the patch where the highest intake rate is expected.

Introduction

Spatial heterogeneity in the abundance of food provides a forager an opportunity to enhance its food intake rate by concentrating foraging effort within profitable areas (Valone & Brown 1989). However, when food items are cryptic this might not be a simple task since the content of patches is not obvious prior to exploitation. We see a patch as a discrete spatial entity of the environment (e.g. a branch for a foraging woodpecker; Olsson *et al.* 1999) or as the spatial entity that is exploited during the time the forager does not move (e.g. the part of the field that is grazed without moving the front legs for an ungulate, also called a foraging station; Focardi, Marcellini & Montanaro 1996).

Basically, there are two ways in which a forager can realize a beneficial skew in the allocation of feeding effort: (i) by regulating the time in patches (Charnov 1976), and (ii) by regulating movement between patches (Walsh 1996). Information about the food distribution is essential in order to regulate time and movement in the most profitable way (Dall *et al.* 2005). A forager can have access to different sources of information about the content of patches. Firstly, a forager acquires information during patch exploitation. This is called 'patch sample information' and it typically includes the number of prey found and the time spent foraging (Valone 1991). Secondly, a forager may have acquired information about characteristics of the food distribution during earlier visits to the habitat. This prior knowledge is called pre-harvest information (Valone 1991). Finally, a forager can perceive information about the quality of patches by monitoring the foraging success of other foragers. This vicarious sampling of resource quality has been termed 'public information' (Valone and Templeton 2002).

In order to be able to regulate the time in the patch a forager in an environment with cryptic food densities has to assess (rather than 'knows') the quality of a patch (Oaten 1977). A faster assessment is beneficial to a forager since less time is devoted to poor patches and more time can be devoted to rich ones (Valone & Brown 1989; Clark & Mangel 1986). Patch assessment is enhanced by combining patch sample information with pre-harvest information, a process called Bayesian updating (Iwasa, Higashi & Yamamura 1981; Green 1984; Olsson & Holmgren 2000; Van Gils *et al.* 2003). In current Bayesian assessment models, the frequency distribution of food densities is considered to be the pre-harvest information the forager has access to (Green 1984; Olsson *et al.* 1999; Van Gils *et al.* 2003). In these models, the probability that a certain food density is encountered is thus equal to the frequency in which this density occurs in the environment. The frequency distribution of food densities is related to spatial variation in the abundance of food. However, this so-called spatial variance is not the only characteristic of a heterogeneous food distribution (Li & Reynolds 1995; Wiens 2000), and is consequently not the only possible source of pre-harvest information. Different food densities are usually not randomly distributed throughout the area, but spatial pattern exists (Li & Reynolds 1995; Wiens 2000). Spatial pattern implies that the probability to encounter a certain density in a nearby patch depends on the

content of the current patch (Mangel & Adler 1994). For example, in a clumped food configuration the probability that a high-density patch is encountered nearby is higher if the density in the current patch is high. Thus, knowledge about the content of a patch provides information about the content of nearby patches. Knowledge about the spatial pattern is another form of pre-harvest information, which can be used to improve patch assessment by a Bayesian forager.

To efficiently regulate its movement, a forager, in an environment with cryptic food densities, should have pre-harvest information on the spatial pattern of the food distribution. A forager that is sensitive to spatial pattern can enhance its intake rate by regulating the length and/or direction of movements between patches to its recent foraging experience. For example, in a clumped food configuration a forager can enhance the encounter rate with high-density patches and avoid area with low-density patches by intensifying search from a high-density patch (shorter movements, increased sinuosity; also called area-restricted search) and weaken search from a low-density patch (longer movements, decreased sinuosity) (Benhamou 1992; Klaassen *et al.* in press *b*).

We are aware of only one study in which an effect of spatial pattern is demonstrated on both patch assessment and movement pattern. Fortin (2003) described foraging behaviour of free ranging Bison *Bos bison*. During winter, Bison dig craters in the snow to reach vegetation. A crater is considered equal to a foraging patch. Movement between patches appears to be non-random and linked to the spatial pattern in vegetation, as suggested by the observation that poor patches are encountered less often than the proportions available. Moreover, it was shown that areas of similar food quality were searched with different intensities, which was explained by differences in recent foraging experiences. The latter result indicates that also the assessment of a patch was affected by spatial pattern in vegetation.

In the current study we explore whether pre-harvest information on spatial pattern affects patch assessment and/or movement patterns in tactile-foraging Mallard *Anas platyrhynchos*. Qualitative theoretical predictions are tested in a laboratory experiment in which Mallard were solitarily foraging in environments with random, clumped and regular spatial distributions of cryptic food densities. To our best knowledge, this study is the first experiment to assess the significance of pre-harvest information about the spatial distribution of food densities on both patch assessment and movement patterns, using contrasting spatial configurations of food densities.

Theoretical predictions

We here introduce two models to illustrate the effects we expect of spatial pattern on patch assessment and on movement pattern. Models provide predictions about assessment and movement for the specific food distributions used in the laboratory experiments. This includes a random, a clumped and a regular configuration of full (20 wheat seeds buried in

sediment) and empty (sediment only) patches. Distributions do not differ in the frequency of full and empty patches, i.e. always half of the patches are full. We describe spatial pattern by so-called structure functions, since this describes spatial pattern from the forager's perspective (Mangel & Adler 1994). A structure function is the probability that a patch at distance i is full, given the state of the current patch (full or empty, Fig. 1). Further details about the food distributions are provided below.

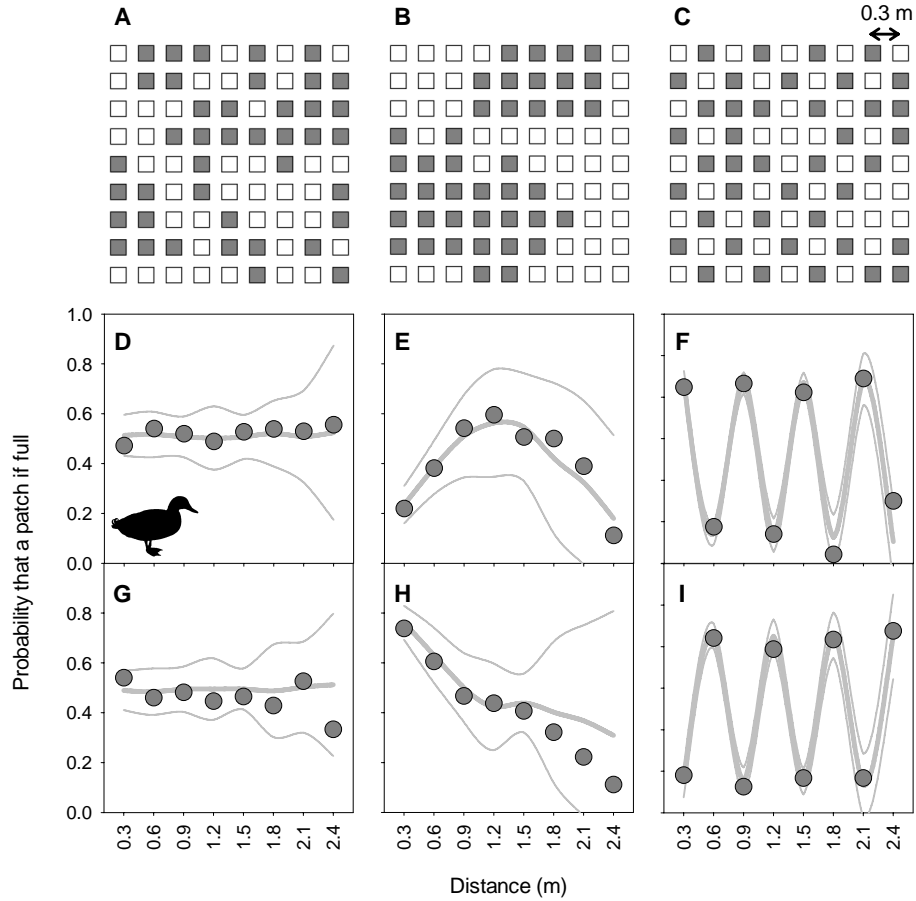


Figure 1. A-C: Examples of a random (A), clumped (B) and regular (C) spatial configuration of full (grey squares) and empty (open squares) food trays. A tray represents a patch for a foraging Mallard. A full patch contains 20 wheat seeds, an empty patch contains no seeds. Distance between the centres of neighbouring patches measures 0.3 m. D-I: Structure functions, i.e. the probability that a patch at distance i from a current patch is full, given that the current patch is empty (upper row, D-F) or that the current patch is full (lower row, G-I). Dots correspond to structure functions for the particular configurations depicted in panels A-C. Grey lines depict average structure functions for the corresponding type of spatial distribution used in this study (thick line is average, thin lines are 95% confidence limits). D&G random, E&F clumped, F&I regular distribution.

Energy expenditures were not considered in the models. To make our point it appeared to be sufficient to derive (qualitative) predictions from gross intake rate estimates, because in this case differences in intake rate are predominantly effectuated by time rather than by energy.

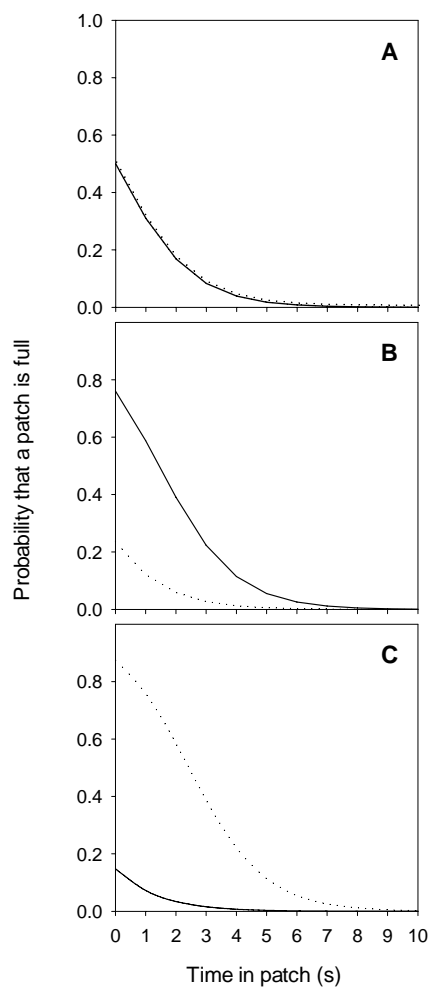


Figure 2. Probability that a patch is full over time in the patch as long as no food item is found, if the previous (neighbouring) patch had been full (solid line) or empty (dotted line). (A) random, (B) clumped and (C) regular spatial configuration of full and empty patches throughout the environment.

(i) Patch assessment model

Seeds are cryptic and we thus assume that a forager is incapable of an instantaneous assessment of the content of a patch upon arrival (Valone & Brown 1989). A forager has a prior expectation about the content of a patch based on pre-harvest information. In a random food distribution spatial pattern contains no information, thus the prior expectation is solely based on pre-harvest information about the frequency distribution of food densities (i.e. spatial variance). In this case, the probability that a patch is full, upon arrival, is 0.5, irrespective the content of the previous patch. In clumped and regular food configurations, there is spatial information, thus the prior expectation about the content of a patch is based on a combination of pre-harvest information about both the frequency and the spatial pattern of densities. In these cases, the probability that a patch is full depends on the content of the (adjacent) previously visited patch, as described by the structure functions (see Fig. 1). For example, for the clumped configuration considered in this study, the probability that a patch is full is 0.76 if the adjacent patch was full and 0.24 if the adjacent patch was empty.

During exploitation the expectation about the content of a patch is continuously updated with patch sample information (Iwasa *et al.* 1981). In our experiment we only have two patch types (empty and full), thus when a forager finds one food item it instantaneously knows that it is in a full patch. It is consequently most interesting to examine how the expectation about the content of a patch develops over time as long as no prey is found. The (posterior) probability that a patch is full (P_{oF}) as a function of time in the patch (t), when no food items are found is (after Olsson 2006):

$$P_{oF}(t) = \frac{P_F \cdot e^{-20At}}{1 - P_F + P_F \cdot e^{-20At}} \quad (1)$$

where P_F is the (prior) probability that the patch is full at $t=0$ (i.e. upon arrival in the patch) and A is the search efficiency ($A=0.04$ patch·s⁻¹, based on the type II functional response with handling time $t_h=0.65$ s as observed in this study). P_F can be derived from the structure function. The expectation that a patch is full, given the incident that no food items are found, decreases over time (Fig. 2). This decrease is more pronounced for the clumped configuration when the previous patch was empty and the regular configuration when the previous patch was full, which is the result of lower P_F 's (Fig. 2).

As pointed out by Green (1984), Olsson & Holmgren (1998), and Olsson & Brown (2006) an assessing forager maximizes its long-term intake rate by leaving a patch as soon as the expected potential intake rate during the remainder of the patch visit drops to a certain critical intake rate C . In order to predict the time a forager spends in an empty patch (patch residence time, PRT), we calculated the potential intake rate over time in a patch from the posterior probability that the patch is full, according to Olsson (2006). Since we are interested in the effect of pre-harvest information about spatial pattern on patch

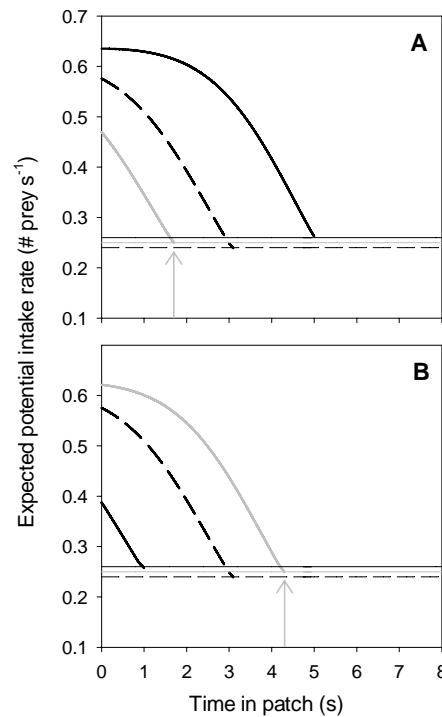


Figure 3. The expected potential intake rate in a patch over time, as long as no food item is found, if the previous (neighbouring) patch had been empty (A) or full (B). The dashed line corresponds to a random configuration, the grey solid line to a clumped configuration, and the black solid line to a regular configuration of full and empty patches. Horizontal lines depict the critical intake rates at which a forager is predicted to leave a patch (dashed line for random, grey line for clumped, and solid line for regular configuration). The grey arrow indicates the time after which a forager is predicted to leave a patch for the clumped food configuration; about 1.7 s when the previous patch had been empty, and about 4.3 s when previous patch had been full.

assessment we calculated the potential intake rate over time for the situation that the previous (neighbouring) patch had been empty (posterior distribution for previous empty patch) and for the situation that the previous patch had been full (posterior distribution for previous full patch). The critical intake rate that maximizes long-term intake rate is different for these situations (except for the random distribution), because these situations represent different environments. We took the average of these critical intake rates as the critical intake rate for the specific spatial distribution, and calculated the potential intake rate over time for the previous patch being empty and for the previous patch being full, for this average critical intake rate. The critical intake rate was 0.24 for the random distribution, 0.26 for the regular distribution, and 0.25 for the clumped distribution. We checked for each

spatial distribution that the intake rate that was achieved by the forager was equal to the specific critical intake rate (results not shown).

For clumped and regular distributions, the time after which the estimate of the potential intake rate reaches the critical level C depends on the content of the previous patch (Fig. 3). Consequently we predict that the time that a forager spends in an empty patch depends on the content of the previous adjacent patch in the clumped and regular, and not in the random distribution. In particular, for the clumped configuration we predict that the PRT in an empty patch is longer if the previous patch had been full than if the previous patch had been empty. In contrast, for the regular configuration we predict that the PRT in an empty patch is longer if the previous patch had been empty than if the previous patch had been full. For the random configuration we predict no differences in PRTs if the previous patch had been full or empty.

(ii) *Inter-patch movement model*

In order to evaluate the optimal movement between patches we calculated the expected gross intake rate over distance (see also Klaassen *et al.* in press *b*). The probability that a patch at distance i is full, given the content of the current patch, is described by the structure functions (Mangel & Adler 1994). Mallard consumed an average of 9 seeds in a full patch (this study), thus we can calculate the expected gross intake in a patch at distance i , given the content of the current patch b (b can be full (F) or empty (E)), by:

$$\hat{n}(i) | b = P(F_i | b) \cdot 9 + P(E_i | b) \cdot 0 \quad (2)$$

which equals:

$$\hat{n}(i) | b = P(F_i | b) \cdot 9 \quad (3)$$

where $P(F_i | b)$ and $P(E_i | b)$ stand for the probability that a patch at distance i is full (F) or empty (E), respectively, conditioned on the content of the current patch, as given by the structure function.

The expected time to travel to and spend in a patch at distance i , given the content of the current patch, is correspondingly calculated by:

$$\hat{t}(i) | b = P(F_i | b) \cdot (t_F + \frac{i}{v}) + P(E_i | b) \cdot (t_E + \frac{i}{v}) \quad (4)$$

where t_F is the time foraging in a full patch (11.22 s, this study), t_E is the time foraging in an empty patch (2.33 s, this study), and v is the velocity of a Mallard (0.25 m·s⁻¹, this study).

Subsequently, we can calculate the expected gross intake rate \hat{N} in a patch at distance i , given the content of the current patch by dividing the expected gross intake by the expected time:

$$\hat{N}(i) | b = \frac{\hat{n}(i) | b}{\hat{t}(i) | b} \quad (5)$$

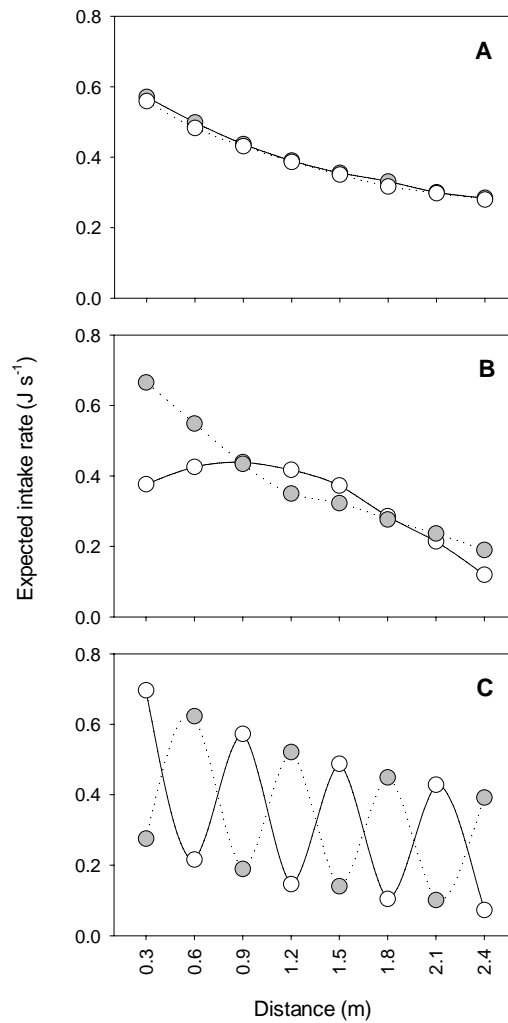


Figure 4. The gross intake rate that is expected in a patch at distance i from the current patch, given that the current patch is empty (open symbols) or that the current patch is full (grey symbols). Different panels relate to different spatial distributions of full and empty patches: (A) random, (B) clumped and (C) regular configuration. Lines and symbols overlap for the random configuration. For the random configuration the highest intake rate is always expected in the neighbouring patch. For the clumped configuration the highest intake rate is expected in the neighbouring patch when the current patch is full, and in the 3rd patch ($i=0.9$) when the current patch is empty. For the regular configuration the highest intake rate is expected in the neighbouring patch when the current patch is empty, and in the 2nd patch ($i=0.6$) when the current patch is full.

The intake rate that a Mallard should expect in a patch at distance i is affected by the content of the current patch in clumped and regular but not in random configurations (Fig. 4). For the random configuration the highest intake rate is always expected in the adjacent patch (Fig. 4). For the clumped configuration the highest intake rate is expected in the adjacent patch if the current patch is full and in a more distant patch if the current patch is empty (Fig. 4). For the regular configuration the highest intake rate is expected in the adjacent patch if the current patch is empty and in a more distant patch if the current patch is full (Fig. 4). Thus a Mallard that moves to the patch where the highest intake rate is expected, is predicted to always move to the adjacent patch in the random configuration, to the adjacent patch if the current patch is full and to a distant patch if the current patch is empty for a clumped configuration, and to the adjacent patch if the current patch is empty and to a distant patch if the current patch is full for a regular configuration (Fig. 4).

Experiments

Food distribution

Food was distributed over 81 plastic trays (12 x 12 x 6 cm), placed in a 9 x 9 array (30 cm between centres of two adjacent trays; examples in Fig. 1; a tray is treated as a foraging patch for a Mallard). All trays were filled with a 4 cm layer of coarse grained sand, and water was added until the water level equalled the level of sand. In half of the trays 20 wheat seeds per tray were buried in the sediment. We checked by visual inspection that seeds did not protrude the sediment in order to ensure that seeds were cryptic to the Mallard.

We created food distributions with random, clumped and regular spatial configurations of full and empty trays, by selectively positioning full and empty trays throughout the array. In a random configuration no spatial relationships exist. In a clumped configuration, a positive spatial autocorrelation exists, whereas in a regular configuration a negative spatial autocorrelation exists (Legendre 1993). Spatial pattern was quantitatively described by Moran's I , a measure of spatial autocorrelation, under the randomization hypothesis using the Rookcase add-in, with adjacency defined as Rook's (Sawada 1999). No significant spatial autocorrelations could be detected for the random configurations (average Moran's I index of 0.4, average $P=0.24$). Spatial autocorrelation was highly significant for all clumped and regular configurations (average Moran's I index of 6.5 and -8.4, respectively, all $P < 0.01$).

Moreover, spatial pattern was described from the perspective of the forager by structure functions (Fig. 1, and Mangel & Adler 1994). Structure functions differed dramatically for different types of spatial distributions (Fig. 1). For random configurations, the probability that a patch was full was about 0.5 for all distances, irrespective the content of the current patch. For clumped configurations, the probability that a patch was full decreased over distance if the current patch was full and increased and subsequently decreased over

distance if the current patch was empty (Fig. 1). Structure functions for regular configurations strongly fluctuate (Fig. 1).

Experimental trials

Experimental trials were conducted from 7 – 26 March 2005 with eight Mallard (four males, four females). Between trials, Mallard were kept in an outside aviary where food (mixture of grains and pellets) was provided after experimental trials for a period of 1 hour. Ducks were feeding solitarily and one trial was performed per duck per day.

Food was offered in the same spatial distribution (random, clumped or regular) to a duck for 6 successive days. After one day without a trial, another type of spatial distribution was offered to the same individual duck for another 6 successive days. Again, after one day without a trial, the remaining spatial distribution was offered to the same duck for another 6 successive days. The order in which different types of spatial distributions were offered to individual ducks was according to a random block design. Configurations with the same spatial distribution differed in the exact position of full and empty patches to avoid that ducks could learn the position of full patches. The structure function of a particular configuration always fell within the 95% confidence limits around the average structure function for that specific distribution (determined by excluding the focal configuration, like in a cross validation, see Fig. 1).

A trial was started at the moment that the duck was released into the experimental room. During a trial a duck was continuously observed from a separate room through a one-way mirror. The order in which food trays were visited was recorded. Furthermore, the whole trial was recorded by a video system. After a duck visited 50 patches or after a period of 15 minutes, whichever was the shortest, a trial was ended. After a trial trays were collected, and the content of all full trays that were visited by the bird was sieved in order to determine the number of seeds eaten (per tray).

Analyses

Video captures were analyzed using The Observer Video-Pro software (Noldus Information Technology, Wageningen, The Netherlands), in which media files were played back at half speed. From these captures we determined for every tray the time feeding in the tray (defined as the time having the tip of the bill below the sediment surface) and the length of the movements to the next tray (defined as the distance between the centres of the current and the next visited tray). Furthermore, for every trial we calculated the gross intake rate the duck achieved by dividing the total number of seeds eaten by the total time feeding and moving.

We restricted the data analyses to the last experimental day of a week (we assume that ducks had learned characteristics of the spatial distribution by this day). Cases related to revisits of patches and cases related to full patches where less than 2 seeds were eaten

were excluded. For the analysis of feeding time in empty patches, we only included cases where the previous and the current patch were adjacent (i.e. 0.3 m between centres of trays). The feeding time in an empty patch was analysed as a function of the food distribution and whether the previous patch was full or empty by general linear modelling (GLM), with 'content of the previous patch' (F or E), 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors. Time in a patch was log transformed to meet model assumptions.

The length of a movement to the next patch, given the spatial pattern of the food distribution and the content of the patch where this movement was started was analysed by GLM, with 'content of the previous patch' (F or E), 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors. Movement lengths were log transformed to meet model assumptions.

The average gross intake rate as a function of the food distribution was analysed by a factorial ANOVA, with 'spatial distribution' (random, clumped or regular) and 'individual duck' as factors. All analyses were conducted using STATISTICA software package version 7.1, StatSoft 2005).

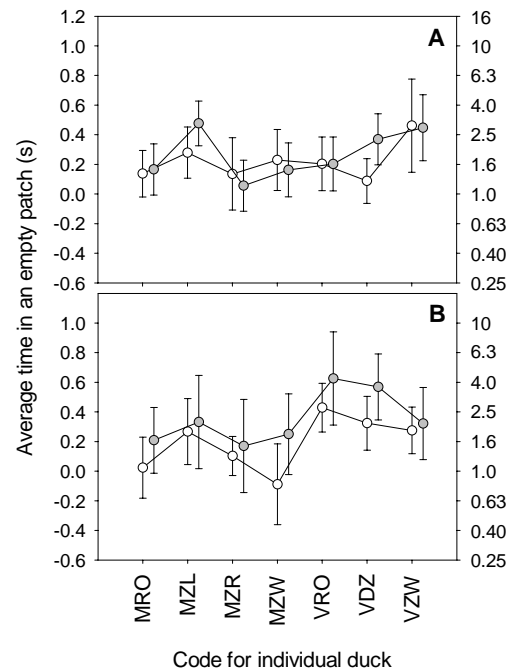


Figure 5. The average time that a Mallard spent in an empty patch after a visit to a neighbouring patch that had been full (filled circles) or that had been empty (open circles) (log-transformed values on left, untransformed values on right axis). Panel A corresponds to an environment with a random and panel B to an environment with a clumped spatial distribution of full and empty patches. Error bars denote 95% confidence limits.

Results

We obtained enough data for the random and clumped distribution for 7 ducks. Data for one female duck were discarded because accidentally a regular instead of a clumped configuration was offered on the 4th day. Naturally, we did not obtain enough data for the regular distribution about the time that ducks spend in empty patches after a visit to an adjacent empty patch due to the fact that such a combination hardly occurs in this distribution. PRTs in empty patches were very different for different individual ducks ($F_{6,194}=4.8$, $P<0.01$, Fig. 5). More importantly, in a clumped environment all ducks spent more time in an empty patch if the previous patch was full than if the previous patch was empty ($F_{1,82}=6.6$, $P=0.01$, Fig. 5A). In a random environment no such effect of the content of a previous patch could be detected ($F_{1,112}=0.9$, $P=0.35$, Fig. 5B).

There was considerably less variation in the length of movements between ducks (no effect of individual: $F_{6,834}=0.5$, $P=0.80$), which is probably caused by the fact that almost all movements (96.3%) were to neighbouring patches. However, the length of a movement to the next patch was significantly affected by the content of the previous patch ($F_{1,834}=7.4$, $P<0.01$) and by the type of spatial distribution ($F_{2,834}=4.7$, $P<0.01$), but the effect of content of a previous patch was not different for different spatial patterns (interaction $F_{2,834}=0.8$, $P=0.45$). For all spatial distributions duck tended to make larger movements from empty than from full patches, and the average length of a movement was largest in clumped and smallest in regular distributions (Fig. 6).

Finally, type of spatial distribution had a significant effect on the average intake rate ($F_{2,12}=4.1$, $P=0.04$). A Tukey post-hoc test revealed that the intake rate in clumped configurations (average $0.43 \text{ seeds}\cdot\text{s}^{-1}$) was significantly higher than in regular configurations (average $0.33 \text{ seeds}\cdot\text{s}^{-1}$; $P=0.04$), and a strong trend existed that it was also higher than in random configurations (average $0.34 \text{ seeds}\cdot\text{s}^{-1}$; $P=0.05$).

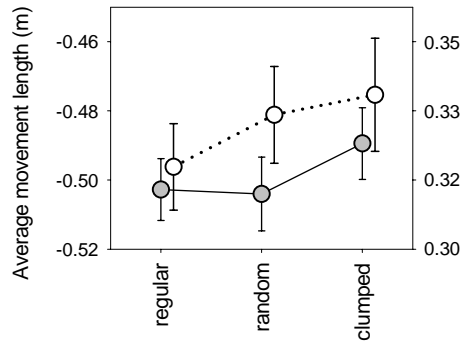


Figure 6. The average length of movements that started in a full patch (grey dots) and or that started in an empty patch (white dots) (log-transformed values on left, untransformed values on right axis), for environments with a regular, random or clumped spatial distribution of full and empty patches. Error bars denote 95% confidence limits.

Discussion

Patch assessment and movement pattern

In accordance to our predictions, Mallard spent less time in an empty patch when the previous (neighbouring) patch had been empty than when the previous patch had been full, in environments with a clumped configuration of food. Such regulation of foraging time was not observed for environments with a random configuration of food densities. Unfortunately, due to the very nature of regular configurations we could not evaluate whether Mallard regulated the time in patches in environments with a regular distribution of food densities. Nevertheless, Mallard appear to be sensitive to spatial pattern in the distribution of food densities, and use this pre-harvest information in their assessment of the content of patches.

There was no consistent agreement between prediction and observation for the length of movements between patches. As predicted for the clumped distribution, a movement that started in an empty patch was larger than a movement that started in a full patch, but a similar response was also observed in the other two spatial distributions where this response was not predicted. It appeared that Mallard in all distributions almost always moved to a neighbouring patch (96.3%).

We conclude that the Mallard in this experiment did learn the spatial pattern in the distribution of food densities, but that this knowledge only affected the assessment of patches and not the movement pattern between patches (at least not according to the predictions). An enhanced assessment in a clumped food distribution seems to be linked to a higher intake rate.

Conditions for regulating inter-patch movement

In this study the Mallard responded to spatial pattern by mainly regulating the time in patches rather than by regulating the movement between patches. In other studies an effect of spatial pattern on the movement pattern was observed (e.g. Smith 1974; Pienkowski 1983; Nolet & Mooij 2002; Fortin 2003; Klaassen, Nolet & Bankert, in press *a*). This raises the question why movement was not so much regulated in this study and why it was regulated in other studies. Obviously, one condition for regulating movement in response to spatial pattern is that the spatial pattern in the distribution of food is non-random. For example the distribution of the food for Canvasbacks *Aythya valisineria* (winter buds of *Vallisneria americana*) appeared to be random (Lovvorn & Gillingham 1996). In a random food distribution knowledge of the content of a patch does not provide information about the content of nearby patches, which prevents any possibility to adjust movement in a profitable way. However, random configurations seem to be the exception rather than the rule, thus in most natural situations there seems to be an opportunity to fine-tune movement.

One possible explanation why such response was not observed in our experiment is that Mallard do not travel to the patch where the highest intake rate is expected, but to the nearest patch where the expected intake rate upon arrival is higher than the critical intake rate. For the clumped distribution used in our experiment, the expected intake rate upon arrival in a patch is always higher than the critical intake rate. This is illustrated in figure 7 where we show how the expected potential intake rate develops over time for patches at a different distance from the previous patch (when no prey is found in the patch, and when the previous patch was empty). This might explain why Mallard in our clumped configuration (almost) always moved to the neighbouring patch, also when the previous patch had been empty. It would consequently be interesting to determine movement patterns of Mallard in a clumped distribution in which the expected intake rate upon arrival in a patch is lower than the critical intake rate. Observing that Mallard skip a patch after an encounter with an empty patch would corroborate the idea that Mallard travel to the nearest patch where the expected intake rate upon arrival is higher than the critical intake rate rather than to the patch where the highest intake rate is expected.

The optimal patch-leaving behaviour (PRT) is different for a solitarily forager, like in our experiment, than for a forager in a group. A forager in a group is under exploitative competition, and then the best tactic is to “catch as catch can”, i.e. to deplete patches down to the *current* average intake rate of the environment rather than down to the final quitting intake rate (Nolet, Klaassen & Mooij 2006). In analogy with these results we might expect that a forager under exploitative competition moves to the patch where the highest intake rate is expected (i.e. is sometimes skipping patches), rather than to the patch where the expected intake rate is higher than the final quitting intake rate. Interestingly, in all cases where an effect of pattern on movement was observed (see above) the foragers were presumably under exploitative competition. An appealing follow-up experiment would be to establish movement patterns for the different spatial distributions for a Mallard that is under exploitative competition, i.e. that is foraging in a group.

Interaction between PRT and movement pattern

A forager maximizes its long-term intake rate by leaving a patch as soon as the expected potential intake rate drops to the maximum average intake rate of the environment (Green 1984; Olsson & Holmgren 1998; Olsson & Brown 2006). Spatial pattern allows a forager to improve patch assessment, and consequently less time is spent in empty and more time is spent in rich patches. A forager can thus achieve a higher intake rate in an environment with spatial pattern, which is reflected in the slightly higher critical intake rates predicted for the clumped and regular distributions (Fig. 3).

Obviously, the critical intake rate depends on the average prey density of the environment, since in an environment that is richer in food a higher average intake rate can be achieved. A forager that does not regulate movement between patches, as observed in

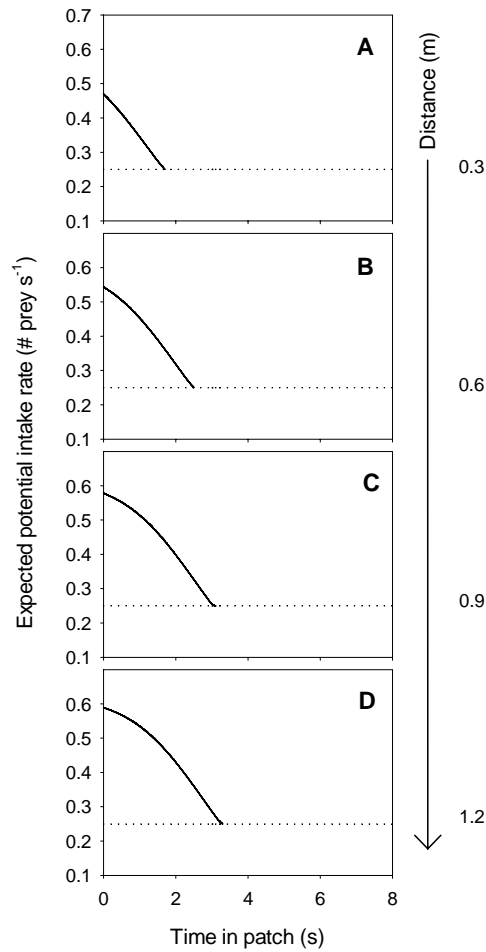


Figure 7. The expected potential intake rate in a patch over time, as long as no food item is found, given that the previous patch had been empty, for an environment with a clumped distribution of full and empty patches. Different panels correspond to different distances from the previous patch, increasing from A (0.3 m, neighbouring patch) to D (1.2 m, 4th patch). The horizontal dotted line indicates the critical intake rate (which maximizes the long-term intake rate, 0.25 prey·s⁻¹) at which patches are left. Note that for these patches the expected intake rate upon arrival in a patch is above the critical intake rate.

this study, encounters full and empty patches in proportion to their availability (Klaassen *et al.* in press *b*). That is why we could take the average of the optimal critical intake rates for the for the situation that the previous patch had been empty and for the situation that the previous patch had been full as the optimal critical intake rate for the specific spatial distribution. However, a forager that moves strategically through an environment with

spatial pattern, encounters empty patches less often and rich patches more often than the proportions these patches occur throughout the environment (Klaassen *et al.* in press *b*). In other words, such forager perceives a much richer environment, and is consequently expected to leave patches at a higher critical intake rate. To calculate the critical intake rate for such situation one should account for the frequency in which full and empty patches are encountered by the forager.

Directions in studies on patch assessment and movement pattern

We can recognise different directions in the study of responses of foragers to spatial variance and spatial pattern in the abundance of food. Firstly, what we like to call 'patch assessment models' describe how a forager can enhance its intake rate by improving patch assessment by combining patch sample information with pre-harvest information about the frequency distribution of food densities (i.e. spatial variance) (Iwasa *et al.* 1981, Green 1984; Olsson *et al.* 1999; Olsson 2006). These models typically assume discrete patches and no spatial pattern in the distribution of densities (random distribution). Furthermore, foragers are assumed to encounter food densities in proportion to their availability since movement between patches is random. A field study on woodpeckers feeding on invertebrate prey and an experimental study with Knots *Calidris canutus* feeding on buried shellfish demonstrated that foragers assess patch quality in close agreement with the model predictions (Olsson *et al.* 1999; Van Gils *et al.* 2003). Olsson *et al.* (1999) do not provide details about the spatial pattern in the distribution of food densities and about the inter-patch movements of woodpeckers. Van Gils *et al.* (2003) ensured that food densities were randomly distributed among patches, according to their model assumptions. Patch assessment models pass over the fact that most natural food distributions are spatially patterned, and that this spatial pattern is another source of pre-harvest information about the content of patches. Hence, a spatially explicit version of this model, as introduced in this paper seems very valuable in predicting PRTs.

Secondly, what we like to call 'movement velocity models' describe how a forager can enhance its intake rate by regulating the velocity of their movement to the spatial pattern in the distribution of food densities (Knoppien & Reddingius 1985; Krakauer & Rodriguez-Girones 1995). These models assume that the environment is continuous, i.e. suitable foraging habitat occurs everywhere throughout the environment. Foragers move through the environment with a certain velocity that is inversely related to the search efficiency (Gendron & Staddon 1983). When a forager moves at a low velocity (intensive search mode) much time is spent at a certain point (that we could consider as a patch, Kacelnik & Bernstein 1988), whereas when a forager moves at a high velocity (extensive search mode) little time is spent at a certain point. Foragers do not regulate the length of inter-patch movements, i.e. they always travel to a neighbouring point. An adaptive response to spatial pattern is realized by adjusting the velocity of movement, and consequently the time in a

patch, to the recent foraging experience. In essence, these models predict the time a forager spends in a patch, given the content of the current patch, and the spatial pattern of the environment. An example of the time spent in a patch in relation to the recent foraging experience and the spatial pattern is provided by Van Gils (2004). He shows that Knots and Great knots *Calidris tenuirostris* spent more time per step (i.e. per patch if we consider the area searched in one step as a patch) close to a captured prey than further away from a captured prey, in a food distribution that was thought to be clumped. 'Movement velocity models' also seem to be applicable for our experimental situation since we only observed an effect of pattern on the time in the patch and not on the movement pattern between patches.

Thirdly, 'two-dimensional movement models' describe how a forager can enhance its intake rate by regulating the sinuosity of the foraging path, in response to spatial pattern in the distribution of food densities (Benhamou 1992; Hill, Burrows & Hughes 2003). As the previous 'movement velocity models' these models assume that the environment is continuous and that foragers invent their patches during foraging (Kacelnik & Bernstein 1988). Foragers regulate the sinuosity of their path based on their recent foraging experience, in relation to the spatial pattern in the food distribution. A fundamental difference with 'patch assessment models' and 'movement velocity models' is that due to their non-random movement rich patches are encountered more frequently and poor patches less frequently than the proportion in which they occur throughout the environment. An application of the model is found in the movement pattern of thrushes, studied by Smith (1974). It was shown that thrushes increased the sinuosity of their path after a capture in a naturally clumped distribution of earthworms. Furthermore, Smith (1974) conducted a series of experiments with artificial food items, and showed that an increase in the sinuosity in the patch was not observed if these artificial food items were regularly distributed. In our experiment Mallard moved in straight lines and only made turns when approaching the edge of the food distribution. Furthermore, the frequency distribution of turning angles was equal for movements from empty and from full patches, for all distributions ($\chi^2_7 < 0.20$, $P > 0.98$ for all distributions). In other words a 'two-dimensional movement model' seems not to be applicable for this particular situation. It remains to be established why foragers adjust the sinuosity of their path in some but not in other cases.

Finally, we recognise 'discrete movement models' that describe how a forager can enhance its intake rate by regulating the length of movements between patches (Klaassen *et al.* in press *b*). A forager estimates the content of patches based on the content of the current patch and the spatial pattern of the food distribution and subsequently travels to the patch where it expects the highest intake rate. When a forager makes a longer movement, the patches in between the current and the distant patch are not visited. This 'skipping' of patches is not considered by the aforementioned models. The movement model used in this study is an example of a 'discrete movement model'. This model is for example applicable

for Bewick's swans *Cygnus columbianus bewickii* feeding on Fennel pondweed tubers *Potamogeton pectinatus* (Klaassen *et al.* in press *a*). Swans dig craters to retrieve the buried tubers (a crater is considered to be a patch). The distances swans swim between craters appeared to be related to the food density in the crater where movements started: swans moved a short distance to the next crater if the food density in the crater had been high, whereas they moved a long distance to the next crater when the food density had been low. This behaviour was thought to enhance the swan's intake rate since the food distribution was clumped. The 'discrete movement model' could not explain movement patterns observed in this experiment. Mallard seemed not to regulate movement patterns in relation to spatial pattern in this experiment.

These models all find their application in specific situations, i.e. each model is useful to interpret and/or predict specific aspects of the patch use and movement behaviour of an intake rate maximizing forager. It seems that there is no general model that grasps all the possible ways in which a forager can respond to spatial variance and spatial pattern in the abundance of food. It is now the challenge to understand why foragers regulate particular aspects in certain but not in other circumstances. This not only needs a detailed review of the different ways different types of foragers respond to spatial heterogeneity, but also detailed experiments that tackle specific questions, similar to this study.

Acknowledgements

We thank Koos Swart, Peter de Vries, Thijs de Boer and Mariska Wagenaar for assistance during the experiment. We thank Ola Olsson for providing the source code of his programme that calculates potential intake rates for a two-patch situation. RK thanks Jan van Gils for motivating discussions and illuminating remarks on an earlier draft. This study was carried out under license CL04-01 of the KNAW animal experiments committee. This is NIOO-KNAW publication xxxx and publication xxxx of the Centre for Wetland Ecology.